J Raptor Res. 28(3):127–133

EFFECT OF NEST-BOX SIZE ON NEST-SITE PREFERENCE AND REPRODUCTION IN AMERICAN KESTRELS

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Abstract.—I studied American kestrels (*Falco sparverius*) in the boreal forest of northern Saskatchewan from 1988–93. These birds preferred nest boxes over ubiquitous natural cavities. Several lines of evidence, including provisioning of boxes late in the breeding season, suggest that nest boxes did not influence population density. On average, natural cavities had less than one-half the basal area of my standard boxes. The potential effect of box size on nest-site preference and on reproduction was tested in two ways: (1) by offering kestrels a choice between two boxes on the same or nearby tree—one of standard size and one with a 50% smaller basal area, (2) by only having small boxes available in one area. Kestrels strongly preferred the larger boxes, but still chose boxes over cavities when only small boxes were available. Predation rate on nests, clutch size, brood size at fledging, and nest success were all unaffected by box size.

Key Words: *American kestrel*; *nest box*; *nest site*; *population*; *reproduction.*

Efecto del tamaño de caja anidera sobre el sitio de nidificación y reproducción de *Falco sparverius*

Resumen.—Estudié *Falco sparverius* en el bosque boreal del norte de Saskatchewan desde 1988 a 1993. Estas aves prefirieron cajas anideras en vez de cavidades naturales. Las evidencias sugieren que, incluyendo un tardío aprovisionamiento de cajas en la estación reproductiva, las cajas anideras no influyeron la densidad poblacional. En promedio las cavidades naturales tenían menos de un medio del área basal de mis cajas estándar. El efecto potencial del tamaño de las cajas sobre la preferencia por sitio de nidificación y reproducción de *F. sparverius,* fue probado de dos maneras: (1) ofreciendo una elección por dos cajas, una de tamaño estándar y otra de un área basal 50% más pequeña, ubicadas en el árbol o muy cercano a él; (2) ofreciendo solamente de cajas pequeñas en una área. *F. sparverius* prefirió claramente las cajas más grandes. Parámetros como tasa de depredación sobre los nidos, tamaño de la nidada y éxito del nido no fueron afectados por el tamaño de la caja.

[Traducción de Ivan Lazo]

The American kestrel (*Falco sparverius*) breeds in such diverse habitats as deserts, the northern treeline, agricultural landscapes, and urban areas, spanning a large proportion of the New World (Cade 1982, Bird 1988). Equally impressive is the diversity of natural nest sites used by this species, including cavities in trees, woodpecker holes, ledges of cliffs, holes in earthen banks, and magpie (*Pica* spp.) nests (Cade 1982, Bird 1988). In addition, the array of artificial nest sites includes boxes, drain pipes, chimneys, abandoned buildings and ledges on tall office buildings of big cities (Bird 1988 pers. obs.). A variety of nest sites occurs within a population, not just among locales. The substantial variability among natural nests makes it difficult to address the question of whether nest boxes are unrepresentative of the natural state (see Møller 1989, 1992). To what natural standard should nest boxes be compared?

An investigation of how nest boxes may influence reproduction and population dynamics is still important for a species like the American kestrel. Despite the extensive use of kestrel boxes, there are few data available on consequences of their use. Research should focus on how nest-site parameters influence breeding biology. This would provide much needed information facilitating the comparison of studies in different areas (Møller 1992). My primary objective was to determine how availability and size of boxes may influence population density, nest-site preference and reproduction.

Methods

Study Area and Population. I studied American kestrels in the vicinity of Besnard Lake, Saskatchewan, Canada (55°N, 106°W), from 1988–1993. The area is boreal forest with an array of forest types and stand ages. The predominant species are trembling aspen (*Populus trem-*

Table 1. Attributes of nest boxes and natural cavities used by American kestrels.

Dimensions	Box[a] Standard	Box[a] Small	Natural Cavity $\bar{x}$	Natural Cavity SD	Natural Cavity Range	Natural Cavity N
Maximum at base (cm)	23.1	16.5	17.0	2.20	14–20	11
Minimum at base (cm)	20.3	14.6	14.7	2.15	14–18	11
Basal area (cm^2)	469	241	198[b]	45.0	137–254	11
Entrance diameter (cm)	7.5	7.5	7.4[c]	2.47	5–12	9

[a] In addition, all boxes were 37 cm deep from the lid or approximately 25 cm deep from the lower edge of the entrance hole.
[b] Derived by the formula for area of a circle or ellipse.
[c] Some data were not available because the cavity broke open at the level of the entrance hole when it fell to the ground. If the hole was elliptical, the maximum dimension was used here.

uloides), jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), black spruce (*P. mariana*), and birch (*Betula* spp.) all of which grow in pure and mixed-species stands. The mosaic of forest ages and species composition is both natural and human-influenced. The virgin forests were extensively logged for pulpwood in the 1970s and 1980s, with a limited amount of cutting for sawtimber within the last few years. Most forestry operations involved clearcutting; however, because jack pine was the only commercial species sought, most areas contain clumps of aspens or other species and so there are almost always scattered trees throughout. There is no agriculture or other major land use in the area.

Breeding kestrels prefer openings in the boreal forest, including clearcuts and natural areas such as muskegs, marshes, and burned forest. They are also common where only small clearings exist such as roadways through forests, and in dense brush and saplings 6 m or more tall. They also nest along undisturbed shorelines of lakes surrounded by continuous, dense virgin forests. I did not study a discrete population limited to nest boxes, but sampled part of a large, contiguous population.

In the summer of 1987 and spring of 1988, I erected 153 nest boxes along a gravel highway and logging roads passing through forests and clearcuts. In subsequent years the study was expanded to 345 boxes spanning approximately 300 km of roadway. Each box represents a potential "territory." Most boxes were nailed approximately 4 m above ground for easy access by ladder, and they faced all compass directions. Boxes were put up in all forest types, but were placed usually on aspens as it was in that species that I observed most cavities. The extent of uncut forest around each box varied. Many boxes were placed at the edge of a forest along a roadway, whereas others were put up in lone, mature trees surrounded by young regeneration following a clearcut.

Kestrels arrived on the study area in mid- to late-April. Most eggs were laid over a 4-wk period beginning in mid-May, and the young fledged from mid-July to mid-August. Box occupancy rate varied from 49 to 62% among years. Kestrels migrated from the area in late August and early September.

Attributes of Cavities and Boxes. I obtained too few data for analysis of reproduction in natural cavities, as most nests were situated in dead trees too tall and dangerous to be climbed. Some nesting cavities fell or were cut down, so I measured their interior dimensions at the base and entrance holes (Table 1). All 11 nests were old woodpecker holes, of which eight were situated in trembling aspens, two in birches, and one in a jack pine.

Nest boxes were made from exterior-grade fir plywood 15 mm thick. Their dimensions were determined primarily for efficiency of cutting plywood (Table 1). Lids were hinged for access from above, and most were stained a pale gray (similar to aspen bark) on the exterior to preserve the wood. A few centimeters of wood shavings were placed in the bottom each fall and spring after the box was cleaned out.

Experiments with Availability and Size of Boxes. As a test of whether nest sites were limited in this population, I erected nest boxes late in the breeding season in an area where there was none. I put up 35 boxes 25 May to 2 June 1988 which corresponded to the mid- to late-laying periods. If the study area contained some birds that were capable of breeding, but were prevented from doing so because of limited nest sites (see Bowman and Bird 1987), then these boxes should be occupied.

I chose basal area as the size variable to test given the large differences between cavities and my boxes (Table 1). In addition, studies have shown that clutch size of raptors (Korpimäki 1985) and passerines (e.g., Karlsson and Nilsson 1977) may respond to the basal area of nest boxes. I tested the preference for and consequences of box size in two ways. First I offered kestrels a choice between two boxes. In an area where boxes had already existed for 1–4 yr, I nailed a second, similar box to an adjacent tree, generally a few meters away, at the same height and orientation. When a suitable tree was unavailable, the same nest tree as the old box was used and I placed the new box above or below the old one. Inside one of each pair of boxes, alternating between new and old, I placed an L-shaped plywood insert that reduced the interior dimensions of the box so that it was similar to those of cavities (Table 1). I refer to these modified boxes as small. This experiment was conducted at 71 sites (potential territories) situated along a gravel highway and four logging trails The distance between adjacent boxes was on average 820 m (SD = 500, N = 58) and the extremes of this portion of the study area were approximately 20 km apart.

A second experiment was conducted in an area of similar

Table 2. Number of active boxes, mean clutch size and success of nest boxes in an area with standard boxes 1988–91 and small boxes 1992–93.

	Box Size					
	Standard				Small	
	1988	1989	1990	1991	1992	1993
N boxes active/available	10/17	15/17	15/17	15/19	15/19	10/19
Clutch size $\bar{x}$ (SD)	5.1 (0.32)	4.7 (0.46)	4.7 (0.70)	4.7 (0.59)	4.8 (0.44)	4.5 (0.53)
N nests successful/failed	7/3	11/3	13/2	6/9	12/2	3/6

nest-box density and located approximately 40 km from the first. I fitted all existing standard boxes (N = 19) with an insert identical to the ones described above. Therefore, there was no choice for box size, and available boxes were similar to the mean size of cavities. My intention was to investigate any changes in reproduction that might be attributed to small boxes compared to the previous 4 years of data collected in this area and on standard boxes elsewhere. I erected new boxes for the choice experiment and installed the inserts in August 1991, and collected data in 1992 and 1993.

Monitoring of Nest Boxes. I visited the boxes approximately every 5–7 d during the pre-laying period. Any whole or partial squirrel nests in the boxes were removed. Adult kestrels were captured on bal-chatri traps or by hand in the nest box. All adults were color-banded and measured upon capture (Bortolotti and Iko 1992). Once eggs were discovered I ceased checking the box until the clutch was complete. I refer to any box that contained eggs or young as being active. The number of eggs laid, hatched, and ultimately the number of young fledged were all documented. Sample sizes are not consistent for all analyses because of missing data, accidents such as trees blowing down, and a loss of road access.

RESULTS

Preference for Boxes and Box Size. Kestrels undoubtedly preferred boxes over natural nest sites, although I did not attempt to find all cavity nests. However, the study area was traversed daily by myself and one or two other field crews and records of all kestrels sighted were kept. Even if all areas between our boxes where kestrels were sighted repeatedly are treated as active natural-cavity sites, which is improbable, then the annual estimate of natural cavity use was only about 5–15%. Color-banding of adults throughout the year helped to confirm the identity of birds using boxes vs. cavities (see also Bortolotti and Iko 1992).

Given that cavities were on average less than half the basal area of the standard nest box (Table 1), size may have been a criterion for nest-site selection. When given a choice between the standard and small box, eggs were most often laid in the larger box. In 1992, 33 (80.5%) of the 41 boxes with eggs were of standard size, while eight (19.5%) were of the small size (G = 14.99, P < 0.001). In 1993, only 2 (6%) of 33 clutches were in small boxes (G = 28.04, P < 0.001).

Size alone is unlikely to explain the selection of boxes over cavities, for there appeared to be no reduction in frequency of box use compared to previous years in the area after all boxes had been converted to the small size (Table 2). The same number of territories were active in 1991 before the experiment, as in 1992 when only small boxes were available. This constancy of occupancy was true for the entire study area as well. In 1993 a reduction in numbers of pairs occurred, but this is consistent with a reduction in use for the entire study area that year. I did not observe pairs at natural cavities in the experimental area in 1993 to account for the difference between years. The consistent use of this area could not be explained by site-tenacity of breeding birds. In 1992 the breeding population of the no-choice experiment was comprised of only 1 of 15 females, and none of 10 males, that had been color-banded as breeders in the area in 1991. Similarly in 1991, when only standard boxes were available, none of 15 females and only one of nine males that nested in the area in 1990, returned to breed there.

Density. Several lines of evidence suggest that natural nest sites were abundant, and the presence of boxes did not increase the density of breeding birds. Even those sites that had been logged contained scattered clumps of mature trees. Woodpeckers, especially the northern flicker (*Colaptes auratus*) and the pileated woodpecker (*Dryocopus pileatus*), were abundant and widely distributed, as were natural cavities in mature trees. Trees immediately adjacent or the nest-box tree itself typically contained apparently suitable cavities. The proximity of consecutive boxes along a road was no closer than what I have observed between active kestrel nests under natural conditions.

That boxes were selected over cavities, rather than boxes being the only nest sites available, is also suggested by observations during the pre-laying period. Color-banded male and female kestrels inspected both cavities and boxes within the same territory, and moved among boxes (see Bortolotti and Iko 1992). In some cases, pairs moved from boxes into cavities apparently as a result of disturbance. From 1991–93 in an area far removed from the box-size experiments, I placed electronic balances inside boxes to monitor laying and incubation behavior (see Bortolotti and Wiebe 1993). I installed balances days to weeks prior to laying within territories occupied by kestrels. Eggs were laid in only 26 of 70 boxes with balances. Pairs at the remaining boxes switched over to nearby cavities, or in some cases left the area, probably because of the alteration to the box or the disturbance required to calibrate the equipment. These observations further suggest that kestrels had a choice of nesting in a box or a tree cavity.

It is plausible that the presence of multiple nest sites could influence the attractiveness of the area for breeding kestrels (Hamerstrom et al. 1973). However, this does not appear to be true for the choice experiment. Of the 71 sites available, eggs were laid in 41 (58%) and 33 (46%) boxes in 1992 and 1993, respectively; this rate is comparable to the 58% occupancy in 1991, the only year prior to the experiment for which the same number of potential territories were available in that area.

It does not appear that this population contained individuals that were prevented from breeding for lack of a nest site, for there was no response to the provisioning of boxes late in the nesting season. Only one late box contained eggs, but this was undoubtedly a renesting attempt; the female's brood patches were already refeathering during laying (see Wiebe and Bortolotti 1993). All of the boxes used in this experiment were active in subsequent years, indicating that they were placed in suitable habitat.

The lack of occupancy of the late boxes in 1988 could be accounted for if kestrels avoided newly made boxes, or if prospecting for boxes in a previous year is important as it is for some cavity-nesting waterfowl (Eadie and Gauthier 1985). Neither seems likely for this population. I also erected 41 identical boxes from 19–21 April 1988. These boxes were "early" in that kestrels were just arriving on the study area. Unlike the late boxes, these early boxes were accepted with a typical occupancy rate (46.3%). Similarly, of 109 "old" boxes, i.e., erected in 1987, 48.8% were active in 1988. Although there were kestrels in the habitat supplied with late boxes, they were likely already committed to a cavity by the time the late boxes became available.

Predation. Predation at kestrel nests was limited to eggs rather than nestlings (Bortolotti et al. 1991) or adults. Depredations were as common in standard boxes (14%) as they were in all small boxes (14%), both years combined. The red squirrel (*Tamiasciurus hudsonicus*) was believed to be largely responsible. These results may not be surprising given that the two box types had the same size of entrance hole (Table 1). Although entrance diameter is usually considered to be relevant to studies of predation, it is not a significant factor here. In this study area there were no large predators, such as raccoons (*Procyon lotor*) that have been problematic in other studies (e.g., Toland and Elder 1987), so any cavity/box entrance big enough for a kestrel was likely big enough for most or all of its egg predators. Also, natural cavities used by kestrels had similar entrance diameters to the nest boxes (Table 1).

Red squirrels, and to a much lesser extent northern flying squirrels (*Glaucomys sabrinus*), may also be competitors for nest sites (see also Balgooyen 1976, Cade 1982, Toland and Elder 1987). Although grassy nests were removed during our visits in the pre-laying period, some were rebuilt and used for rearing young. Squirrels built nests at 31 of a possible 142 sites in the choice experiment over the 2 yr. Grass was found in both boxes at eight sites, in the small box only at 12 sites, and in the standard box only in 11 other sites; therefore, the kestrels' choice of larger boxes was not apparently related to squirrel activity.

Reproduction. There was no apparent relationship between basal area of the box and clutch size (Table 3). The standard boxes of the choice experiment had a mean clutch size of 4.7 eggs (SD = 0.53, $N = 58$) that was the same as all small boxes combined ($\bar{x} = 4.7$, SD = 0.45, $N = 29$). There was no significant difference between the number of large (five and six eggs) and small (three and four eggs) clutches in the standard and small boxes ($G = 0.03$, $P > 0.5$). There also seemed to be no response in clutch size to small boxes in the area where there was no choice when compared among years (Table 2).

Unlike clutch size, the success with which pairs fledged one or more young varied greatly among years (see also Hamerstrom et al. 1973); however, there was still no apparent effect of box size. A comparison of the data for 1988–1993 in the no-choice experiment shows that the 2 yr of small boxes were among the best and worst (Table 2). In the choice experiment of 1992, 22 (67%) of 31 nests in standard-size boxes were successful, while four (50%) of the eight small boxes were successful (Fisher's Exact Test $P = 0.40$). In 1993, nest success over the entire study area was the poorest to date. The two small boxes active in the choice experiment of 1993 became inaccessible shortly after hatching because of a road washing out, and so the only comparison between standard and small is between areas with and without a choice of box size. Only eight (35%) of 23 nests were successful in standard boxes of the choice experiment. Similarly, only three (33%) of nine were successful in the area where there was no choice except small boxes.

The number of young fledged per successful nest also was unaffected by the size of the nest box. In 1992 the three small boxes in the choice experiment fledged four, four, and three young, respectively, while the standard boxes fledged a mean of 3.9 (SD = 1.30, $N = 18$). A mean brood size of 3.9 (SD = 0.96, $N = 15$) was also true for all small boxes of 1992 combined. In 1993, the standard boxes fledged on average 2.1 young (SD = 1.26, $N = 8$), while the three small boxes in the no-choice area fledged one, two and three young, respectively. Collectively, these data do not suggest that box size had any influence on nesting productivity.

Table 3. Frequency of clutches of different sizes in nest boxes of different size and experimental treatment 1992 and 1993.

		CLUTCH SIZE			
EXPERIMENT	BOX SIZE	3	4	5	6
Choice	Standard	1	16	40	1
	Small	0	0	6	0
No choice	Small	0	8	15	0

DISCUSSION

The American kestrels in this forested region may be different from many of those studied elsewhere in that they appeared to have considerable choice of potential nest sites. The experimental provisioning of boxes late in the season, the abundance of cavities, the presence of many unused nest boxes, and behavioral observations all suggest that these birds had many potential places to breed. Size appeared to be an important criterion for nest-site selection given the preference for standard over small boxes. Kestrels also seemed to prefer the larger of two nest boxes intended for ducks (Gauthier 1988). Oddly, this preference was not associated with any reproductive advantage (e.g., Tables 2 and 3). The effect of box size on reproduction has also been tested on kestrels in captivity with the same negative results (David M. Bird pers. comm.). These findings give support to the validity of comparing nest-box-based studies of kestrels. It is more problematic determining the consequences of the use of boxes versus cavities, and why boxes are so attractive.

To some degree, reproduction of American kestrels in boxes and cavities has been addressed elsewhere. Craig and Trost (1979) and Toland and Elder (1987) found no differences in productivity in a comparison of boxes and natural sites in Idaho and Missouri, respectively. The usual practice by researchers of cleaning out nest boxes, while of concern for some species (Møller 1989), may be unimportant for kestrels. Heintzelman (1971) found that hatching success and nestling survival were not reduced when kestrels used boxes that had not been cleaned after a previous year's use. Similarly, Balgooyen (1976) did not attribute any losses of young to disease and parasites associated with the species' lack of nest sanitation in natural cavities.

The universal effect that provisioning of boxes seems to have is to increase the nesting density of a kestrel population (reviewed by Toland and Elder 1987, Bird 1988). My study may be unusual in that there is no evidence that density increased with nest box use. Similarly, densities did not increase in two species of cavity-nesting owls supplied with boxes (data from this symposium).

A preference of boxes over cavities, even when the latter are available, appears to exist in this and other kestrel populations (Cade 1982, Toland and Elder 1987) and other species (e.g., Brawn 1988). There is no clear explanation for this. Although my standard nest boxes were substantially larger than the cavities kestrels had used (Table 1), size alone cannot account for the strong preference for boxes over natural nests. Kestrels consistently used boxes even when all available boxes were reduced to a size that made them comparable to cavities (Table 2).

The Saskatchewan kestrels could not have preferred boxes because they themselves were raised in them or had previous successful nesting experience with them. Prior to 1993, my students and I banded over 3300 kestrels. Only about 15% of our color-marked adults have ever been seen again in the years subsequent to their capture. Similar to other kestrel populations (Bowman et al. 1987), less than 3% of the nestlings banded ever returned to breed; therefore, only about 5% of the population each year was comprised of birds that had been reared in boxes.

One attribute of boxes that is unlikely to explain their desirability is their height above ground. Other studies have shown kestrels prefer higher nest sites (Brauning 1983, Toland and Elder 1987). Although I did not measure any heights of cavities, none that I have seen has been as low as my boxes. Usually cavities were two to three times higher than my boxes.

Three remaining variables seem most plausible to explain the box preference of kestrels: dryness, thermal regime, and light levels. Both nest boxes and cavities (see Balgooyen 1976) can be soaked by rain. It would seem likely that natural cavities would, however, be preferred for rain enters the joints of boxes as well as the entrance holes (pers. obs.). The thermal dynamics of the nest site are potentially important, especially in this high-latitude population. Again, however, one might think cavities would be preferred because of the more insulated, thick walls of the nest site. Alternatively, the thin walls of the nest box may allow for rapid solar heating.

The last, and perhaps the most likely, explanation for box preference concerns light levels. Boxes would almost certainly be brighter environments than cavities. Light can enter through the joints of boxes, and perhaps the thinner wall at the entrance hole, relative to that of a cavity, allows for light to reach deeper into the box. Darkness of the nest interior influences box preference in some birds, e.g., European starlings (*Sturnus vulgaris*; Lumsden 1976). Curley et al. (1987) found that active nest boxes of kestrels had significantly higher reflected light levels than those of the same design used by starlings. They suggested that starlings competed more aggressively for dark boxes, rather than kestrels preferring bright ones. However, it is equally plausible that kestrels chose the boxes with more light. Cavities chosen by kestrels to nest in are known to be nonrandom with respect to orientation. It appears that nest sites with an east-facing direction are often favored (Balgooyen 1976, Raphael 1985). Balgooyen (1976) proposed that such selection had thermal advantages (but see Raphael 1985); however, the directions favored by kestrels would also provide the nest with a maximum amount of sunshine (Curley et al. 1987). A brighter nest interior could have a variety of advantages for parents by giving them better visibility of their eggs and young. I have also seen prey remains in nests, even during times of food shortage, apparently lost in the dark mire that accumulated in the bottom of the box. Higher light levels may reduce food loss, or at least facilitate parents feeding young, offspring self feeding, and perhaps some social interactions.

There are many physical attributes of nest boxes and manners in which the boxes can be made available that may potentially influence reproduction and population dynamics. Testing all of them for a species with such broad natural nesting habits as the American kestrel is problematic. A danger exists in that researchers may become overwhelmed by the variety of alternatives to the point where the study of nest box parameters becomes an end, rather than a means, of investigating meaningful questions in the species' biology. The scope of such research must be limited. Experimental design is thus crucial and depends on the availability of population-specific data. The consequences of artificial nests can only be assessed properly after preliminary data on the behavior and ecology of a population have been collected.

ACKNOWLEDGMENTS

This work was supported by a research grant from the Natural Sciences and Engineering Research Council of Canada, and student support from the Northern Scientific Training Program. I appreciate the cooperation of Saskatchewan Natural Resources for permits. I thank my graduate students K. Wiebe, R. Dawson, and W. Iko, and many field assistants, for their important contribution to the kestrel project. I thank H. Trueman, D.M. Bird, K. Wiebe and R. Dawson for comments on the manuscript.

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Received 3 December 1993; accepted 10 February 1994